Protoplasm and its history.[1]

GEORGE L. GOODALE.

In the department of biology there are three subjects of transcendent interest, namely, protoplasm, or living-matter, development, and adaptation. In fact the interest in some phases of these subjects is now so general and deep that the special students in this department feel that they have to a great extent the sympathy and cooperation of the public at large. This interest renders possible the construction of such commodious laboratories as this, the latest acquisition of the University of Toronto, in which we are now permitted to meet. The generous halls and adequate equipment of this laboratory and other biological laboratories throughout our country and Europe, testify to the existence of a wide-spread belief that the new natural history has very much to learn and much to teach in regard to many of the great problems of life.

In the annual gatherings of the members of our section for the exchange of views and for better fellowship, it has been found expedient for us to look at one or the other of these three subjects at the outset of our work, in a somewhat broad and yet special manner.

Your chairman for the present year asks the privilege of selecting, as his topic for the introductory address, the first of the subjects mentioned. You are invited to examine the more recent additions to our knowledge of protoplasm, restricting the examination to discoveries in the field of botany.

Whether we consider protoplasm, or the living-matter of plants and animals, from the point of view of physics, of chemistry, of physiology, or of philosophy, we have before us a topic which has received, and which continues to receive, the most assiduous attention. Hence its literature, though comparatively recent, is appallingly voluminous, and any attempt to treat the subject, or any considerable part of it, exhaustively, within the limits properly imposed upon introduc-

[1]Address delivered by Professor George L. Goodale, of Harvard University, as Vice-President of the Biological Section of the A. A. A. S., at Toronto, August 28, 1889.

tory addresses, would result in annoyance to you and utter discomfiture for me. Apropos of this, I am reminded of a series of experiments upon protoplasm, conducted in a German laboratory, which will illustrate the embarassment which the case presents. The study to which I refer was with regard to certain organisms of very low grade. At a given period in the life of these organisms, their microscopic masses of protoplasm become confluent in such abundance that sufficient material can be procured for experiments on a large scale. In the special investigation referred to, a considerable quantity of protoplasm obtained in this way was subjected to enormous pressure. You can anticipate the result, there remained behind only a shrunken residue of what we may call, without figure of speech, the most juiceless and the driest of husks.

This natural result of extreme compression has stared me in the face during the preparation of the present address. A similar result is more than likely to follow my attempt to bring within very narrow limits the subject which I have chosen for your consideration.

The word protoplasm was coined by Hugo von Mohl in order to designate certain active contents of the vegetable cell.

We shall gain in clearness of vision by letting our glance rest first on the results of investigating vegetable cells and cell contents, anterior to von Mohl's time, in order that we may see some of the steps by which this term was reached by him. The compound microscope was not applied seriously to the examination of the structure of plants until about fifty years after its discovery by Drebbel. In 1667, Robert Hooke, of England, published an account of his investigations of minerals, plants and animals under the microscope, and gave excellent illustrations of what he thought he saw. His first reference to the structure of plants is in his description of charcoal, and this is followed by a good account of common cork. In these brief and fairly accurate descriptions, the author makes use of the word "*cell*," applying the term to the cavities in charcoal and in cork.

Hooke's interesting treatise was soon followed by two remarkable memoirs—one by an Italian, the other by an Englishman. Malpighi, of Bologna, sent to the Royal Society of London, in 1670, a work entitled *Anatome Plantarum*. The published volumes bear the dates 1675 and 1679. At the period these volumes were in the hands of the Royal Society, Nehemiah Grew, secretary of the Society, was engaged

in work almost identical with that of Malpighi, but there is no good reason to believe, as was formerly intimated, that he was indebted to Malpighi for any of the statements which he published as his own.   It is, however, best for us to consider these two works together.   By Grew the term " cell " appears to have been applied to the cavities in what we may term the softer tissues of the plant.   It is certain that neither Malpighi nor Grew recognized, as we can now, the multifarious forms of vessels, fibres, long cells and the like, as referable to a common source.   There is always a strong temptation to read in an old text some meaning which squares with our own notions, and one is greatly tempted to think that these assiduous investigators, Grew and Malpighi, detected the relationships which we know exist between the different elements of vegetable structure.   But after giving them the benefit of every doubt, one fails to find in their writings any recognition of such affinities.   On the contrary, these investigators were engaged in a study which naturally led them away from such conceptions.   They were busy with descriptive work, outlining the arrangement of tissues in all organs of the plant which their knives could reach.   They did not even break up the tissues into elementary parts, but they described and delineated with great skill the tissues as they were displayed in sections.   Is it not incredible that these first works on vegetable structure, prepared only a few years after the earliest application of the compound microscope to the study of plants, should have remained for almost one hundred and fifty years the only comprehensive treatises on the subject?   But the most charitable inquirer fails to find, during that long period, any other works of importance on vegetable anatomy.

Near the close of the last century, at a period characterized by activity in many departments of speculative inquiries, the subject of vegetable structure again excited considerable attention, but little substantial advance was made.   In 1804 the Royal Society of Sciences at Göttingen proposed for competition certain questions relative to the structure and the mode of growth of tissues.   The chief contestants for this prize were Link, Rudolphi and Treviranus.   The memoirs of the first two received the prize, that of the latter honorable mention.   The names of others should be referred to as having worked at or about this time in the same field, namely : Bernhardi, Mirbel, and Moldenhawer, the latter making a great advance in certain directions. But to all of these whom I have mentioned, including the winners of the prize, the important questions seem to be, how are the structural elements

distributed, rather than how they are related to each other in manner of growth and as respects their origin. With the cell contents they had comparatively little to do. They were busy with the constituents of the framework.

There appears to have been a strong suspicion on the part of some botanists during that period that all this study of the skeleton of the plant failed to go to the bottom of the question. The only wonder is that with their scanty and untrustworthy chemical appliances and with their very imperfect lenses they accomplished so much. May I remind you that the element iodine, which is the most important reagent in the examination of the contents of vegetable cells, was not employed until the year 1812; and, further, that no good achromatic and aplanatic lenses, of even moderately high power, were constructed until 1827.

Noting the more important discoveries of the next period in their order, we come first upon that of the nucleus of vegetable cells by Robert Brown in 1833, and one mode of cell division by Mohl in 1835. In 1838, the eccentric Schleiden published his Contributions to Phytogenesis, in which he states substantially that cells of plants can be formed only in a fluid containing, as chief ingredients, sugar and mucus (*schleim*). By this latter term he designated the nitrogenous matters taken collectively. At his touch all disguises fell, and for the first time the vegetable cell was distinctly recognized as a unit of structure always serving as the common basis for the formation of the innumerable shapes of the structural elements.

Next comes the master, Mohl. Armed with the best optical appliance procurable, familiar with the use of the chemical reagents then at command, and accustomed to accurate research, he reviews his own earlier work and that of his contemporaries, making rapid advance in the knowledge of the contents of the cell. In 1844, in a paper on the circulation within vegetable cells, he speaks of the living mass in each active cell, and distinctly recognizes it as that which is the treasury of stored energy and the vehicle of energy under release. He describes it as that which builds shapely forms out of unformed matter and at first hands. This substance he names *protoplasma*.[2]

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[2] "Da wie schon bemerkt diese zähe Flüssigkeit überall, wo Zellen entstehen sollen, den ersten, die künftigen Zellen andeutenden festen Bildungen vorausgeht, da wir ferner annehmen müssen dass dieselbe das Material für die Bildung des Nucleus und des Primordialschlauches liefert, indem diese nicht nur in der nächsten räumlichen Verbindung mit derselben stehen, sondern auch auf Jod auf analoge, Weise reagiren, das also ihre Organisation der Process ist, welcher die Entstehung der neuen Zelle einleitet, so mag es wohl gerechtfertigt sein, wenn ich zur Bezeichnung dieser Substanz eine auf diese physiologische Function sich beziehende Benennung in dem Worte *Protoplasma* vorschlage."

If we look at the hand-books of botany just before this date of the early forties, we find references to "coagulable matters" (Treviranus), and the chemical instability of the substance within cells was suspected of having much to do with its activity, but almost all of the notes, as well as those upon the same subject found here and there in philosophical writings of the latter part of the last century, are based on pure speculation. The scientific recognition of a physical basis of vital activity must be credited to Schleiden and Mohl.

The term protoplasm was at once adopted by Schleiden, and a good substitute for the indefinite and misleading word *schleim*, which he had employed to designate essentially the same substance, and it became thoroughly established in scientific terminology. In 1850, Prof. Cohn (and Unger in 1855) showed that the protoplasm of vegetable cells is identical with what had been described, in 1835, in animal structures as *sarcode* by Dujardin, and this prepared the way for the exhaustive treatise by Max Schultze in 1858. From that date on, work in the contiguous fields of botany and zoölogy has made no physical or chemical distinction between the living-matter in animals and plants. Investigators in the two fields have been mutually helpful.

Mohl, in his treatise on the vegetable cell, published in 1851, gives the following account of protoplasm :

"If a tissue composed of young cells be left some time in alcohol, or treated with nitric or muriatic acid, a very thin, finely granular membrane becomes detached from the inside of the walls of the cells, in the form of a closed vesicle, which becomes more or less contracted, and consequently removes all the contents of the cell which are enclosed in this vesicle from the wall of the cell. Reasons hereafter to be discussed have led me to call this inner cell the *primordial utricle* (*primordialschlauch*). * * * In the center of the young cell, with rare exceptions, lies the so-called *nucleus cellulæ* of Robert Brown ('*Zellen-kern*'; '*Cytoblast*' of Schleiden). * * * The remainder of the cell is more or less densely filled with an opaque, viscid fluid of a white color, having granules intermingled in it, which fluid I call *protoplasm*."

We must now pass without notice numerous contributions to the subject and consider Hofmeister's description of protoplasm given in his Vegetable Cell, published in 1867.

"The substance protoplasm, whose peculiar behavior initiates all new development, is everywhere an essentially

homogeneous body. It is a viscid fluid containing much water, having parts easily motile, capable of swelling, and possessing in a remarkable degree the properties of a colloid It is a mixture of different organic matters, among which albuminoids and members of the dextrine group are always present. It has the consistence of a more or less thick mucus, and is not miscible with water to any great extent."

From these accounts we see that the following points were regarded as established: (1) All of the activities of the vegetable cell are manifested in its protoplasmic contents. (2) Protoplasm consists chemically of a nitrogenous basis. (3) Protoplasm has no demonstrable structure. (4) The protoplasmic contents in one vegetable cell are not connected with the protoplasmic contents in adjoining cells. (5) The nucleus and other vitalized granules in the vegetable cell are formed by differentiation from amorphous protoplasm.

It is now our duty to see in what manner these views have been modified during the last twenty, or rather ten, years. In describing the changes of opinion, time will not suffice for us to allude to most of the observers; a few only can be mentioned by name.

The first thesis, namely, that all of the activities of the vegetable cell are manifested in its protoplasmic contents, may be regarded as firmly established. It is at this point in our present examination when, if we had time, we should take up, one by one, the terms which have been applied to some parts of what Mohl and Hofmeister knew as protoplasm. But we can only glance at them in passing: Thus, *cytoplasma* is understood to be the mass exclusive of the granular contents of all kinds; *hyaloplasma* is the outer hyaline layer; *polioplasma* is the grayish granular part. To these terms may be added others, such as *paraplasma*, etc.

The second thesis, viz., protoplasm consists chemically of a nitrogenous basis, remains unchanged. But, instead of regarding the protoplasmic basis as comparatively simple, it is now known to be exceedingly complex, and to contain numerous cognate proteids, some of which can be identified in the basic mass, others in the nucleus, and others still in the vitalized granules.

These researches must be considered also with reference to those by two active investigators, Pfeffer and de Vries. The former has shown the conditions under which active protoplasm reacts in the presence of certain chemical ex-

citants, the latter has demonstrated the relations of a part of this irritability of protoplasm to its physical constitution. But, as a result of all these recent studies, it becomes more and more clear that the chemical relations of the proto-plasmic activities are still veiled in mystery. Botanists are receding from a position held by many only a few years ago, namely, that it is safe to use the words albuminoids and pro-toplasm interchangeably ; nowadays the latter term is gener-ally restricted to morphological and physiological concep-tions, the former keeps its wide chemical significance.

Just here come in the chemical studies of protoplasm ; by Rodewald and Reinke on a large scale, by Loew and Bo-korny, and by Schwarz under the microscope. All of these results compel us to recognize in protoplasm a substance of bewildering complexity of composition and constitution. Moreover, you all know how wide this field of research has suddenly become by the discovery that different microbes (which are, essentially, minutest masses of protoplasm) not only give rise to such diverse products, among others the ptomaines, but present such diverse chemical reacitons.

Protoplasm is no longer regarded by any one in any sense as a comparatively simple substance.

The third thesis, namely, protoplasm has no demonstrable structure, has been modified in a striking manner as a result of improved appliances for research. By better methods of staining, and by the use of homogeneous immersion objectives, the apparently structureless mass is seen to be made up of parts which are easily distinguishable. There has been, and in fact is now, a suspicion that some of these appearances, under the influence of staining agents, are post-mortem changes and do not belong to protoplasm in a living state. But it seems to be beyond reasonable doubt that protoplasm is marvellously complex in its morphological and physical as well as its chemical constitution. One statement of the case is as follows :

Under ordinary circumstances, protoplasm is composed of a mesh of inconceivable fineness, in which mesh are en-tangled the more liquid interfilar portions (paraplasma) ; so that the dry husks left in Reinke's experiment may be re-garded as the residue of network from which all the moisture has been expelled. But this conception of protoplasm as a mass composed of a network of minutest fibers enclosing in the meshes another substance, presents, as has been well shown by some critics, great difficulties when we endeavor

to explain the movements within the cell. It is very difficult to explain in any way the so-called wandering of protoplasm outside the cell wall or into intercellular spaces.

Fourth, we are to glance at the accepted statement that the protoplasmic body or protoplast, as it is called, of one cell is cut off by the cell wall from all connection with the contiguous cells. There are a few cases in which this intervening wall was formerly held to be pervious, but such cases were considered as exceptional. Now, however, as has been shown by Gardiner and others who have followed out his exact researches, there are intercommunicating threads of protoplasm of extreme fineness between adjoining cells, and these living threads maintain connections, sometimes direct, sometimes indirect, between one protoplasmic mass and another. This has been shown to be so widely true in the case of the plants hitherto investigated, that the generalization has been ventured on, that *all the protoplasm throughout the plant is continuous*. The formation of the dividing wall in cell division is now better understood than ever before, and our knowledge of this process lends great probability to the truth of the general statement made. It is not unlikely, then, that all the living-matter throughout each plant is continuous, a whole, shut off at the time of severing from the mother plant from the body of protoplasm there, and thus making a true chain of descent.

May I ask you to observe, in passing, how this bears on the vexed subject of individuality of plants. Brücke, in 1862, declared that the living protoplasmic contents of a cell formed an elementary organism, and this idea found its fullest expression in the profound work by Hanstein in 1880. In that treatise Hanstein proposed for the living protoplasmic contents of the cell the term protoplast, in order to indicate its individuality. But these late researches show that these protoplasts are not only highly organized and of complicated structure, but each is bound by indissoluble ties to its nearest neighbors, each helping to form a united whole.

The fifth thesis has been completely controverted. Instead of believing, as formerly, that all the granules within the cell arise *de novo* from the protoplasm in which they are imbedded, we are now forced to regard all of them as springing from pre-existent bodies of the same character.

Hofmeister, in 1867, in an exhaustive description of the contents of vegetable cells, states distinctly that the nucleus arises from homogeneous protoplasm, and that in all cell

division the nucleus must first disappear, two new ones aris-
ing in its place.   The nucleus occupied a secondary place as
a derivative organ.   And the chlorophyll granules were be-
lieved by him and his contemporaries to be new formations
from homogeneous protoplasm under certain conditions of
light, temperature and food.   Researches, which leave no
room for doubt, have shown that the nucleus, in all cases
hitherto examined, springs from a pre-existent nucleus by
a process of division.   The process of division, with its mar-
velous sequence of formal arrangements of definite portions
in meridional lines and in polar and equatorial masses, has
been most carefully examined in almost every organ of the
plant, and in connection with similar processes of cell-divis-
ion in animal tissues.   In no well marked case has a nucleus
been observed to arise from homogeneous protoplasm, even
a few doubtful instances having been lately explained satis-
factorily.

The extraordinary manner in which the nucleus, both in
common cell-division and in reproductive blending, carries
ancestral characters and controls the distribution of nutri-
tive materials, is as yet the greatest mystery in vegetable
life.

We pass next to consider a very important change of
view in regard to the other granules imbedded in the proto-
plasmic body, known as leaf-green or chlorophyll granules.
Formerly, as we have noticed, it was held that all of these
sprang by a process of differentiation from the shapeless mass
in each exposed cell.   Researches by Schmitz on some of
the lower plants, and by Schimper and Meyer on the higher,
have shown beyond any reasonable doubt that these chloro-
phyll granules always arise by a process of division from pre-
existent granules.   But this fact, taken by itself, might not
possess great interest.   It is, however, known that at the
growing points where leaves are developed, the cells contain
in their protoplasm granules of about the consistence and
color of protoplasm itself, and these granules have the power
of division, much after the fashion of the cell nucleus.   But
the products of such division are essentially three-fold ; some
of the resulting granules are colorless, like the mother gran-
ules, others become true chlorophyll granules, while others
still, in those leaves which become the leaves of the flower
and the fruit, assume colors other than green.   In other
words, we have in these associated granules, or chromato-
phores, a morphology which is of the highest interest.   The

needs of the plant bring from this common source the microscopic organs for assimilation, for storing up starch in the form of grains, for protection and attraction. This most interesting generalization in regard to the granules taken together, adds a new zest to the study of the developing plant and the evolving species.

It has been lately claimed by de Vries of Holland, that the sap-cavities or vacuoles in protoplasm divide in much the same way as do the granules just referred to, but this part of the subject is not yet beyond all doubt. That the sap cavities are the birthplace of most crystals, and that the aleurone grains may be desiccated sap cavities has been made out by several observers. But it is not clear that vacuoles divide as granules do. What we do know beyond all reasonable question is this—that all the working granules within the plant have sprung from pre-existent granules, and that there is no break here in the transmission from parent to offspring.

Such, then, are some of the more important changes which have taken place with regard to our knowledge of the living contents of vegetable cells. I would gladly take the time, if it could be granted, to call your attention to certain most interesting discoveries which have been made by Pfeffer relative to the absorption of coloring agents by living protoplasm, and which have been supplemented by Campbell in regard to the nucleus. But more than this allusion is now impossible.

It is an interesting coincidence that with the substitution of the crude compound microscope for high power simple lenses in 1660, came the first works on vegetable structure, and for more than one hundred years, or until the introduction of achromatic object glasses, these works were in truth the only authoritative treatises. With the introduction of water-immersion lenses came renewed activity in this field, and with the later discovery of homogeneous immersion lenses came the results which have now been detailed. Whether we have, at these stages, more than a series of interesting and very striking coincidences, or not, we have not time now to discuss. It is enough for our present purpose to observe that, with the introduction of the cedar oil immersion objectives, a thorough reinvestigation of certain parts of this subject began. One may be pardoned for asking whether the objectives known as apochromatics are to open up in this field new lines of research.

Can these recent discoveries relative to the continuity of

protoplasm and the genetic relationship of the associated granules (including, in the widest sense, the nucleus), be made to cast any light on the question of development, as they certainly do upon the kindred question of adaptation? The answer has been given us very lately by Hugo de Vries of Amsterdam. This investigator, who has done very much to clear up certain obscurities in regard to the external relations of the cell, has recently revised the neglected doctrine of pangenesis and applied it to the question just propounded. De Vries suggests that we divide the hypothesis of pangenesis as proposed by Darwin into two parts, as follows: (1) In every germ-cell individual characters of the whole organism are represented by material particles which, by their multiplication, transmit to descendants all of such peculiarities. (2) All the cells of the organism throw off, at certain periods of development, such material particles, which flow towards the germ-cells, supplying its deficiencies. Now de Vries asks whether it is not high time for us to look at the first part of this hypothesis again, and abandon the hindrances which the latter part imposes. If we accept his suggestion, and restate the hypothesis, in view of what has been learned relative to the nucleus and other granules (the trophoplasts) within the cell, we should then read:

In every cell at a growing part are all the elements ready for multiplication. Each protoplast possesses the organs necessary for continuous transmission; the nucleus for new nuclei, the trophoplasts for new granules of all kinds according to the needs of the plant.

The author reviews the theories bearing on the question from the so-called plastidules of Elsberg to the germ-plasma of Weismann, and then applies his hypotheses of intra-cellular pangenesis to the different parts of a single plant and to the transmission of peculiarities. The active particles recognized in Darwin's hypothesis he terms *pangens*, and, regarding them as vehicles of hereditary characters, traces them throughout their course. He is not obliged to ask for any means of transportation for these pangens, for they work, so to speak, on the spot. They are ready at hand at the points of growth. We must look very sharply with reference to this at two points of growth in the flowering plant, namely: the bud and the seed. Each bud, with its growing point made up of cells containing in their protoplasm the divisible granules, carries with itself all the peculiarities which have been transmitted without appreciable change. In the formation of the

bud there is fission, but no blending. The cells divide, and each new one may in turn divide until the ultimate form of the leafy branch or flower is reached. In the leafy branch new buds form, and in their turn carry forward the ancestral pecu- liarities. But in the flower, on the other hand, with the forma- tion of the ovule, all development is arrested (except in the rare cases of parthenogenesis and the like) unless the protoplasm of the embryonal sac receives a new impetus from material con- tributed by the pollen grain. And in this blending of parts which have developed under different external conditions, we see that there is a chance for variation to come in. Not only is there a blending of the nuclei, but a sharing of the accompany- ing trophoplasts. How this can be applied to the lower plants and other organisms can not now be referred to. It would not be right to hold de Vries wholly responsible for the application just given, but I ask you whether the hypothesis does not ap- pear fruitful. It seems likely to stimulate speculation and further research in this important field.

In view of de Vries' work, and of the results of recent study, which I have endeavored to bring before you this afternoon, does not the statement of Darwin possess new force?

"An organic being is a microcosm, a little universe formed of a host of self-propagating organisms inconceivably minute and as numerous as the stars in heaven."

Cambridge, Mass.

Paraguay and its flora. II.

THOMAS MORONG.

It would be out of place in an article like this for me to attempt to enumerate even a tithe of the trees found in these dense Paraguayan forests, but among those best known abroad are the India-rubber (Siphonia elastica), Erythroxy- lon Coca, logwood (Hæmatoxylon Campechianum), Salix Humboldtii, Carica Papaya, Quillaia saponaria, Fabiana imbricata, Nectandra, Franciscea uniflora, the Omber (Pir- cunia dioica), and Juga dulcis. Something of their charac- ter and numbers may be seen in the collection of her woods which Paraguay has sent to the present Exposition at Paris. The collection is in part composed of one made several years since for a similar exhibition at Montevideo, to which large additions have been made by Dr. Emile Hassler, who has